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Dynamics of twolined chestnut borer *Agrilus bilineatus* as influenced by defoliation and selection thinning

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Abstract

1 The twolined chestnut borer, *Agrilus bilineatus* (Coleoptera: Buprestidae), is a major mortality agent of stressed oak trees. However, patterns of abundance and population change are not well understood.

2 We studied the spatial and temporal variation in abundance of twolined chestnut borer adults during a gypsy moth, *Lymantria dispar* (Lepidoptera: Lymnatriidae), outbreak and examined the influence of both defoliation and thinning on twolined chestnut borer abundance.

3 In stands that were defoliated by gypsy moth, extensive defoliation occurred in one year, and major overstory tree mortality followed in the next. Most mortality occurred in the year preceding the peak year of twolined chestnut borer abundance and abundance of twolined chestnut borer was positively associated with defoliation and mortality in the previous year.

4 Twolined chestnut borers were more frequently associated with poor or fair crown condition trees than trees with good crown condition and were more abundant on members of the red oak group than the white oak group.

Keywords *Agrilus bilineatus*, Buprestidae, defoliation, gypsy moth, *Lymantria dispar*, oak forest, silviculture, twolined chestnut borer.

Introduction

Prior to the infamous demise of American chestnut (*Castanea dentata* [Marshall]) caused by the introduction of chestnut blight into North America (*Cryphonectria parasitica* [Murrill]) *c.* 1904, entomologists noted substantial injury and mortality of that tree species as early as 1891. The twolined chestnut borer, *Agrilus bilineatus* (Weber), was identified as the agent of this mortality and was purportedly responsible for the death of 75% of the chestnut trees in Fairfax County, Virginia, alone, in 1893 (Chittenden, 1909). Although largely ignored in the intervening decades, twolined chestnut borer has been documented as a cause of mortality among oaks (*Quercus,* spp.) (e.g. Côté & Allen, 1980; Haack & Benjamin, 1982). Despite the potential significance of the twolined chestnut borer as a major mortality agent of the dominant species group in forests of eastern North America, much remains unknown about the basic ecology and dynamics of this insect.

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The flathead borers (family Buprestidae) include several destructive species, but in general little is known about the population dynamics of this group in North America. The two most notable among the > 161 species of *Agrilus* are the twolined chestnut borer and bronze birch borer (*A. anxius* Gory) (Arnett, 1993). The life history of the twolined chestnut borer has been described by Côté (1976) and Haack & Acciavatti (1992). Twolined chestnut borer adults feed on foliage after emergence in the spring and move down the tree to mate and lay eggs. When eggs hatch (approximately mid-summer), larvae bore through the bark, construct galleries, and consequently damage cambium. Larvae overwinter in the bark of the tree. Adult twolined chestnut borers attack oaks that have been stressed, often by drought or defoliation. Tree mortality typically occurs after two or three successive years of infestation, but can occur in the first year of attack (Haack & Acciavatti, 1992).

Expansion of the range of the gypsy moth (*Lymantria dispar* L.), a major defoliator of oak in the eastern United States, as well as the incidence of widespread oak mortality (oak decline, *sensu* Staley, 1965 and Wargo *et al*., 1983) has created renewed interest in mortality agents of oak. The gypsy moth is a primary agent of stress to oaks, and attack by twolined chestnut borer or

Armillaria, spp. (shoestring fungus) as secondary mortality agents typically follow defoliation (Wargo, 1977). The roles played by secondary mortality agents such as twolined chestnut borer or *Armillaria* in tree mortality during gypsy moth outbreaks are not completely understood. Numerical increases in twolined chestnut borer have occurred in trees stressed by girdling (Côté & Allen, 1980; Dunn *et al*., 1986), but no conclusive effect of defoliation on twolined chestnut borer has been demonstrated. In this study we examined the temporal sequence of twolined chestnut borer abundance preceding and throughout a gypsy moth outbreak, and we quantified tree mortality relative to twolined chestnut borer dynamics. Additionally, we investigated how thinning a forest in advance of gypsy moth defoliation influenced the interactions of defoliation, twolined chestnut borer dynamics and tree mortality.

We addressed these questions by measuring twolined chestnut borer populations over a 6-year period in stands that experienced a severe outbreak of the gypsy moth. We simultaneously sampled nearby stands with minimal gypsy moth defoliation. This paper, therefore, presents information that distinguishes endemic from epidemic populations of twolined chestnut borer.

Materials and methods

The study took place on the West Virginia University Forest (WVUF), located in Monongalia and Preston Counties, West Virginia, U.S.A. This 3075-ha oak-mixed hardwood forest is located 12 km north-east of Morgantown, West Virginia, along the Chestnut Ridge anticline, in the Appalachian Plateau physiographic province. The average elevation is 590 m. Overstory vegetation varies from stands with a diverse assemblage of mixed-hardwood species to stands dominated by oak. Sixteen stands were selected for this study in 1989. Stands were selected as pairs that were adjacent and had similar overstory composition and site characteristics. The 16 forest stands (eight pairs) that we studied ranged in size from 7.8 to 12.6 ha, with an average size of 10.5 ha and the entire collection of stands were within 5 km.

Within each of the 16 stands, 0.4-ha^2 plots were located along a grid; each plot was separated by at least 100 m. The number of plots in each stand ranged from 10 to 19, depending on stand size (Table 1). The boles of two oak trees, near, but outside the plot perimeter, were wrapped with a 23-cm wide band of resin-coated paper, covered with Tanglefoot^{TM}. The bands were placed approximately 1.4 m above ground. We avoided trees within the plots, as these used for overstory defoliation, vigour and mortality measurements, and placing bands around plot trees may have interfered with accurate overstory mortality estimates. Bands were placed on trees in early to mid-May, and the diameter and tree species were recorded at that time. Tree species sampled were red oak (*Q. rubra*), white oak (*Q. alba*), chestnut oak (*Q. prinus*), scarlet oak (*Q. coccinea*) and black oak (*Q. velutina*). Twolined chestnut borer adults usually initiate flight in late May or early June. The crown condition of each sampled tree, i.e. good, fair, or poor, was noted in 1992, 1993 and 1994. Bands were removed in mid-August of each year, and the twolined chestnut borer adults were removed and counted at that time.

When this study began in 1989, the stands were several kilometres west of the expanding gypsy moth outbreak front. By 1990, gypsy moth populations had quickly risen to outbreak densities, and in both 1990 and 1991 populations on certain areas of the WVUF were very high (Liebhold *et al*., 1998). Populations collapsed however, in 1992 because of an NPV (nucleopolyhedrosis virus) epizootic (Liebhold *et al*., 1998).

During winter 1989–90, eight of the 16 stands were thinned to reduce susceptibility and/or vulnerability to the gypsy moth

Table 1 Descriptions of 16 stands at the WVUF from two time periods: pre-thinning (1989) and immediately following selection thinning (winter of 1989–90). Also included is the percent of preferred species representing suitability to gypsy moth defoliation. Defoliation occurred in six of these stands in 1990 and 1991. Twolined chestnut borer measurements were completed in 1994. Stands followed by the letter ‘T’ indicate a thinned stand. Defoliated stands are noted with an asterisk.

			Before thinning		After thinning	
Stand	Area (ha)	Number of plots	Basal area (m^2/ha)	Preferred species %	Basal area (m^2/ha)	Preferred species %
1 – T	12.2	15	33.8	42	23.8	35
2	11.2	12	31.1	32	–	–
3 – T	12.6	15	34.6	39	24.4	34
4	11.6	15	31.2	40	–	–
5	11.7	14	31.7	34	–	–
6 – T	10.8	14	33.4	11	22.7	12
7 – T*	9.0	11	30.6	41	24.6	35
8*	7.9	11	25.6	52	–	–
9 – T	9.2	10	31.2	60	20.0	65
10	9.8	11	31.1	48	–	–
11 – T	9.7	12	29.2	55	18.2	53
12	9.9	12	28.7	51	–	–
13 – T*	7.8	10	30.0	81	20.3	85
14*	8.0	10	28.2	79	–	–
15 – T*	12.4	19	28.5	67	19.2	68
16*	11.7	13	28.2	79	–	–

(Table 1). One stand from each pair was thinned in accordance with guidelines developed by Gottschalk (1993). The range of basal area removed was 7–12 m^2/ha. The objective of the thinnings was to remove host species of the gypsy moth and to remove trees of low vigour. During the summer of 1990 and 1991 six of the stands (three pairs of thinned and unthinned stands) were defoliated by the gypsy moth (Fig. 1). Each of the six stands incurred > 50% defoliation of preferred species, and > 40% defoliation of all hardwood species for 2 years. Defoliation in the other stands, i.e. background defoliation level, was < 15% of foliage on all species, including the preferred species. Twolined chestnut borer data from 1989 therefore represented base-line information prior to both thinning and defoliation. Twolined chestnut borer collections were repeated in 1991, 1992, 1993 and 1994. To adjust for variation in tree diameter, abundance of twolined chestnut borer was expressed on a per m^2 basis. Collections of twolined chestnut borer on sticky bands were not made in 1990.

All trees on each 0.4-ha plot (an average of approximately 500 trees for each stand) were examined visually for defoliation each year. Estimates of defoliation were made in mid-June, after peak defoliation by the gypsy moth and before refoliation. Defoliation estimates presented in this paper do not reflect canopy loss of the individual trees that were used for twolined chestnut borer sampling; rather, the estimates represented plot-wide and stand-wide defoliation.

The relationship between defoliation and twolined chestnut borer abundance was examined using data among plots, within stands (plot-level) and among stands (stand-level). The relationship between mortality and twolined chestnut borer also was examined at both the plot and stand level. For both defoliation and mortality plot-level data, we used correlation analysis. For the correlation analysis, we considered twolined chestnut borer abundance data from 1992 only, when borers were most abundant. For the stand-level data we used linear regression to test the relationship between twolined chestnut borer abundance, and defoliation and mortality in the previous year. The effect of thinning on this relationship was tested by comparing the confidence intervals (derived from estimates and standard errors) for the slopes and intercepts. We used analysis of variance to examine the effect of thinning in all stands, including stands that were not defoliated.

Analysis of covariance was used to assess the effect of species and crown class on twolined chestnut borer abundance. Least-squared means were compared after adjusting for the effect of defoliation as a covariate. Least-squared means were used

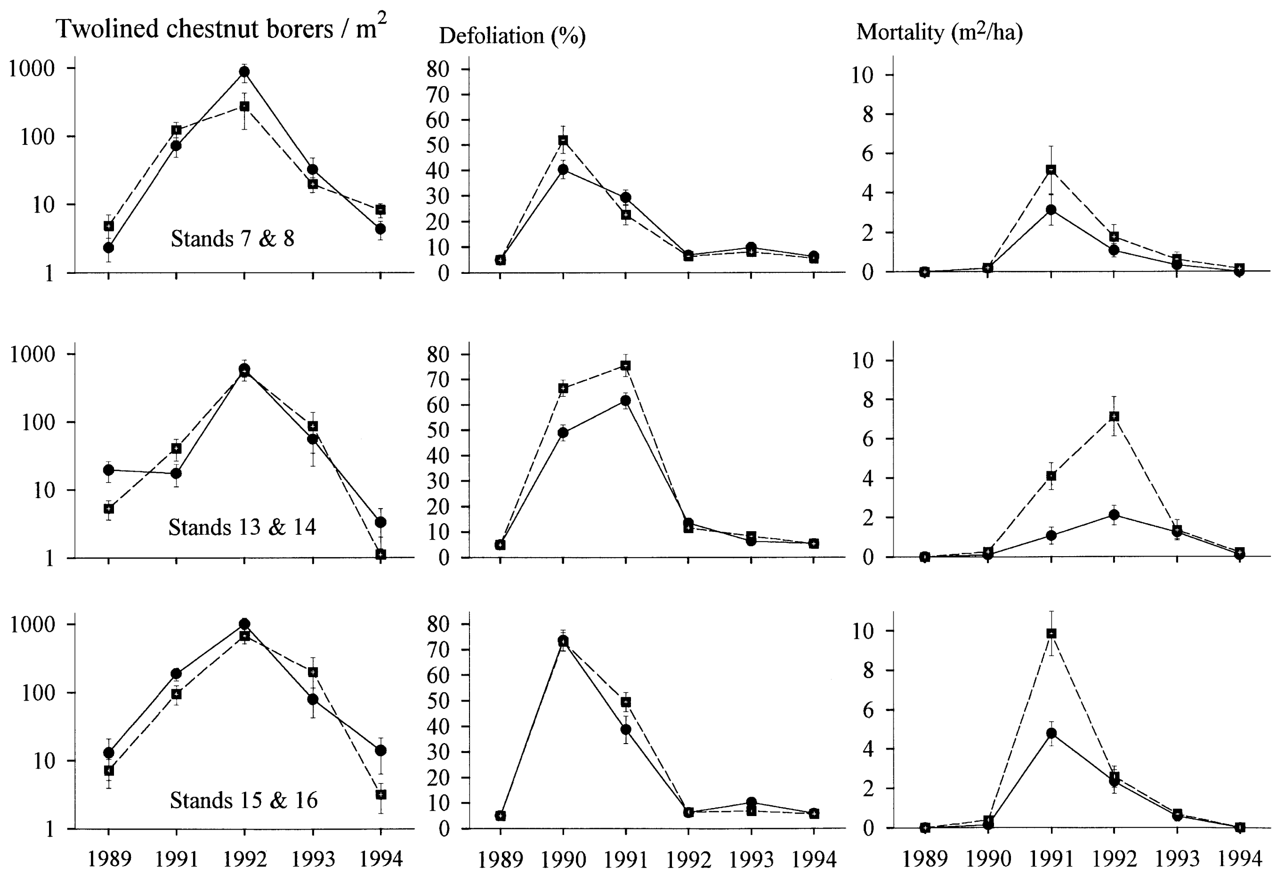

Figure 1 Defoliation on overstory trees (%), mortality of overstory trees (m^2/ha) and twolined chestnut borer abundance (± SE) in three pairs, one thinned and one unthinned in each pair, of defoliated stands on the West Virginia University Forest. Stands were thinned in winter of 1989–90 and defoliation by gypsy moth occurred in 1990 and 1991. No twolined chestnut borer data were collected in 1990. Solid lines and circle symbols represent thinned and defoliated stands; dashed lines and square symbols represent stands that were defoliated only.

Table 2 Average number of twolined chestnut borer/m^2 in each of four treatment types at the WVUF from 1989 to 1994. Stands were thinned in the winter of 1989–90.

	Number of twolined chestnut borers/m^2 of sample area				
Stand type	1989	1991	1992	1993	1994
Undefoliated – Unthinned	12.33	3.27	16.96	20.19	6.90
Undefoliated – Thinned	8.68	30.36	50.87	19.14	2.82
Defoliated – Unthinned	5.69	85.78	533.34	92.89	4.47
Defoliated and Thinned	11.91	111.23	899.31	65.64	7.65

because these removed the effect of defoliation that might have otherwise obscured the influence of crown condition.

Results

Temporal patterns

The average density in 1989, across all stands was 9.2 twolined chestnut borers/m^2. Twolined chestnut borer abundance increased dramatically in 1991, the second year of collection, primarily in stands that were defoliated (Fig. 1). Analysis of variance indicated that both year ($P = 0.0001$) and defoliation ($P = 0.0001$) significantly affected twolined chestnut borer abundance, but thinning ($P = 0.1539$) had no effect. Average pre-thinning abundance of twolined chestnut borer was similar in undefoliated stands (Table 2). There were slight increases in the undefoliated, thinned stands. During the subsequent 2 years most stands had slightly increased numbers of twolined chestnut borers, relative to 1989 values and, except for stands that were neither thinned nor defoliated, twolined chestnut borers were most abundant in 1992 (Table 2). By 1993 the levels had declined in many stands compared with 1989 values, and remained low in the last year of sampling, 1994.

Effect of defoliation

Twolined chestnut borer abundance increased dramatically in defoliated stands one year after defoliation. Six stands were substantially defoliated in 1990 and 1991 (Fig. 1) and abundance of twolined chestnut borer in these stands was greatest in 1992. Over the 6-year period, trends of twolined chestnut borer abundance were similar in paired thinned and unthinned stands, except that twolined chestnut borer abundance was significantly greater in the stand 7 (thinned) than stand 8 (unthinned) in 1992 ($P = 0.013$).

Although temporal trends in twolined chestnut borer abundance at the stand level suggested a strong relationship with defoliation, spatial correlation between defoliation and twolined chestnut was significant at the plot level at only one stand. There was a significant positive correlation between 1992 twolined chestnut borer abundance in stand 8 and defoliation in 1990, 1991 and 1992 (Table 3).

At the plot level, the twolined chestnut borer data were derived from two trees at each plot, and sampling error at this scale may have obscured a relationship between defoliation and twolined chestnut borer abundance. To compensate for this, all the plot data were pooled to establish a composite stand-level estimate of twolined chestnut borer abundance. Corresponding with these data, defoliation values were averaged across individual stands. Stand-level correlations revealed a stronger relationship between defoliation in the previous year and twolined chestnut borer abundance in the current year (Fig. 2).

Table 3 Pearson correlation coefficients of 1992 twolined chestnut borer abundance with defoliation for the six stands on the WVUF that were defoliated. Stand numbers followed by the letter T indicate the stand was thinned in the winter of 1989–90. These correlations were based on data from each plot. An asterisk indicates a significant correlation at $P < 0.01$.

	Year of defoliation		
Stand	1990	1991	1992
7 – T	−0.143	−0.549	−0.185
8	0.409*	0.801*	0.630*
13 – T	0.093	−0.155	0.072
14	−0.103	−0.529	−0.275
15 – T	−0.252	0.084	0.268
16	−0.141	0.190	0.065

Influence on overstory mortality

In order to determine the relationship between twolined chestnut borer abundance and overstory mortality, we compared the 1992 twolined chestnut borer density at the plot level in defoliated stands with the overstory mortality each year (Table 4). Twolined chestnut borer populations in 1992 were significantly and positively related to overstory mortality in Stands 8, 14 and 15. Both 1992 and 1993 mortalities were related to twolined chestnut borer abundance in Stand 8, but only 1992 mortality was significant in Stand 14. In Stand 15, mortality in 1991, 1992 and 1993 was related positively to twolined chestnut borer in 1992.

As with defoliation, we also examined the relationship between twolined chestnut borer abundance and overstory mortality on a stand-level basis (Fig. 3). There was a stronger relationship between twolined chestnut borer abundance and overstory mortality in general on thinned vs. unthinned stands. Thinned stands tended to have more twolined chestnut borer than unthinned stands, but intercepts were not significantly different (Fig. 3). At low levels of overstory mortality, abundance of twolined chestnut borer was the same, irrespective of thinning.

Species and vigour differences

As previous year's defoliation was strongly associated with twolined chestnut borer abundance, we used analysis of

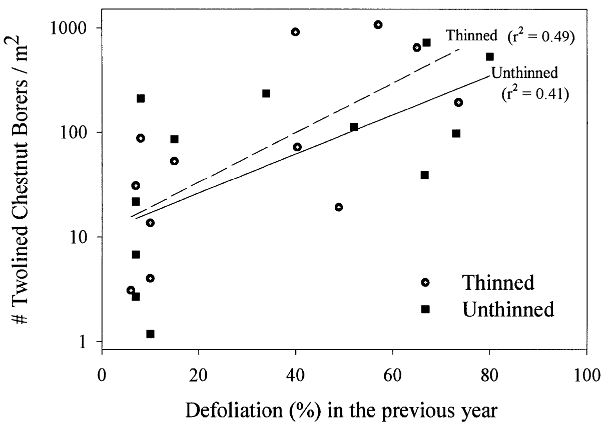

Figure 2 Linear regression of twolined chestnut borer abundance ($\log_{10}$ transformed) on previous year's defoliation (%), averaged for each of six defoliated stands on the WVUF. For unthinned stands, intercept = 1.044 ± 0.33; slope = 0.0187 ± 0.007, F = 6.691, P = 0.027; for thinned stands, intercept = 1.048 ± 0.307; slope = 0.0237 ± 0.008, F = 9.483, P = 0.018.

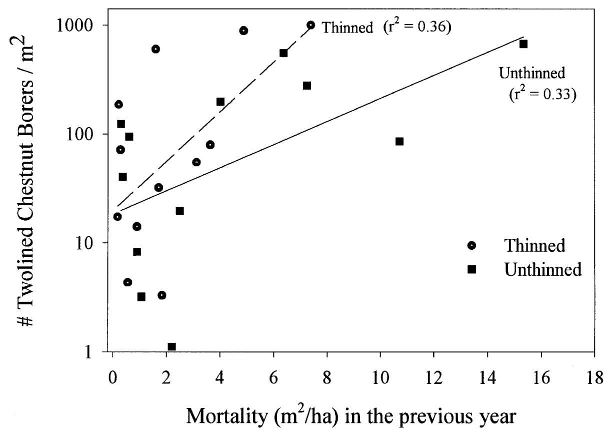

Figure 3 Linear regression of twolined chestnut borer abundance ($\log_{10}$ transformed) on previous year's mortality (m^2/ha), averaged for each of six defoliated stands on the WVUF. For unthinned stands, intercept = 1.269 ± 0.298; slope = 0.106 ± 0.048, F = 9.420, P = 0.001; for thinned stands, intercept = 1.300 ± 0.293; slope 0.227 ± 0.096, F = 10.971, P = 0.013.

Table 4 Pearson correlation coefficients of 1992 twolined chestnut borer abundance with overstory mortality for the six stands on the WVUF that were defoliated. These correlations were based on data from each plot. Stand numbers followed by the letter T indicate the stand was thinned in the winter of 1989–90. An asterisk indicates a significant correlation at $P < 0.01$.

	Year of overstory mortality				
Stand	1990	1991	1992	1993	1994
7 – T	−0.348	−0.417	0.186	−0.371	–
8	−0.302	0.368	0.715*	0.895*	−0.231
13 – T	−0.341	−0.246	0.211	0.017	−0.203
14	0.330	0.016	0.446*	−0.405	0.381
15 – T	−0.393	0.550*	0.752*	0.555*	
16	−0.140	−0.091	−0.001	−0.332	0.006 −0.231

Table 5 Least squares means of twolined chestnut borer abundance on different species groups of varying crown condition. The values were adjusted for the covariate: previous year's defoliation. Values (excluding means) followed by the same letter within a column are not significantly different ($P < 0.01$). The overall species group means are significantly different (P = 0.0091).

	Least-squares means		
Crown condition	White oak group	Red oak group	Mean
Good	0.7758 [a]	0.7405 [a]	0.7581 [a]
Fair	1.0288 [a]	1.5067 [b]	1.2678 [b]
Poor	1.0489 [a]	1.3019 [b]	1.1755 [b]
Overall species group mean	0.9512	1.1831	

covariance, with defoliation in the previous year as the covariate, to examine differences among species and crown conditions. We assigned the five oak species sampled to either the red oak group (*Quercus*, section *Lobatae*) or white oak group (*Quercus*, section *Quercus*). Both the main effects of crown condition and species group were significant as were the interactions. The mean values (Table 5) indicate that twolined chestnut borer abundance was greater on red oaks than white oaks, and greater on trees with fair crown conditions than trees with poor crown condition. As expected, trees with good crown condition had the fewest twolined chestnut borers. The overall results were not entirely consistent with the results from within-species groups. There were no significant differences in abundance of twolined chestnut borer among crown condition classes for the white oak group, but red oaks in good crown condition had significantly fewer twolined chestnut borers than other red oaks.

Discussion

This study supports the claim that stress to trees, as a result of defoliation, can be an inciting factor contributing to increased abundance of twolined chestnut borer. Côté (1976) consistently trapped fewer than 20 twolined chestnut borer/m^2 from unstressed trees in New York, but observed counts of 32–2059 twolined chestnut borers/m^2 on girdled trees in the same study area. In the same study, however, in a nearby area of north-eastern Pennsylvania, traps on unstressed trees yielded 36–749 twolined chestnut borer/m^2, but 750–7046/m^2 from girdled trees. Haack & Benjamin (1982) collected an average of 73 twolined chestnut borers/m^2 in Wisconsin, but an average of 299/m^2 on the same trees a year later, after girdling. In our study, counts of twolined chestnut borer at endemic levels ranged from 1 to 30/m^2. During 1992, when twolined chestnut borers were most abundant on the WVUF, we found a range from 8 borers/m^2 in stand 4, an unthinned and undefoliated stand, to 1004 borers/m^2 in stand 15, a thinned and defoliated stand. Abundance of twolined chestnut borers continued to increase the following year on 15 of the 16 stands, but the increase was most notable in the defoliated stands. It is apparent that defoliation of stands, regardless of thinning, accounted for great increases in twolined chestnut borer adults.

Although gypsy moth defoliation was minimal in 10 stands of the 16, there was an apparent increase in twolined chestnut borers in thinned, undefoliated stands (Table 2). The increase was of a magnitude less than the defoliated stands, and was temporary. The stress from a stand-wide thinning may have reduced the vigour in some individual trees, such that twolined chestnut borers were attracted to the stand and/or attacks were more successful. Logging-related injuries represent another form of stress that may attract twolined chestnut borer adults in a similar manner as girdling (Dunbar & Stephens, 1976; Côté & Allen, 1980). In unthinned, undefoliated stands, the absence of stress is reflected by a decrease in the numbers of twolined chestnut borer in 1991 from 1989.

Within stands there appeared to be only a weak relationship between defoliation and twolined chestnut borer abundance. In the most heavily defoliated stands there was no consistent relationship between defoliation and twolined chestnut borer abundance on a plot level basis (see Table 3). The lack of a consistent relationship between defoliation and twolined chestnut borer abundance may have been due to in part to the random dispersal within stands (among plots) of twolined chestnut borer adults. Dispersal within a stand would conceal any relationship between defoliation and twolined chestnut borer abundance or between mortality and twolined chestnut borer abundance, when analysed at the plot level. At the stand level, however, an obvious relationship existed between twolined chestnut borer and defoliation (Fig. 2), and twolined chestnut borer and mortality (Fig. 3). The existence of these relationships at the stand level and the lack of a pronounced increase in twolined chestnut borer at nearby, non-defoliated stands (Table 2) indicated that dispersal among stands was minimal, despite the potential for substantial within-stand dispersal.

For two of the three pairs of defoliated stands, defoliation was most severe in 1990, overstory mortality was greatest in 1991, and twolined chestnut borer adult abundance was greatest in 1992. The causal relationship this pattern suggests is that defoliation results in overstory mortality the year following peak defoliation, at the levels we observed. Although twolined chestnut borer became more abundant in the year succeeding greatest mortality, that does not preclude twolined chestnut borer from being the mortality agent. The overstory mortality may in part be due to the increasing populations of twolined chestnut borers during the year. Overstory mortality, particularly those trees that died over the course of a growing season, creates an opportunity for elevating populations of twolined chestnut borer, both by attraction and serving as brood trees. A tree with fair crown condition early in the season may serve as an attractant for large numbers of twolined chestnut borers and the tree may eventually die by the end of the season. Twolined chestnut borer is the first beetle to attack stressed oaks, and if mortality is not caused by the borer alone, several other wood-boring insects exacerbate tree stress and contribute to mortality following twolined chestnut borer infestation (Haack *et al*., 1983).

Injured or stressed oaks are attacked preferentially by twolined chestnut borer (Dunbar & Stephens, 1976; Côté & Allen, 1980), and Dunn *et al*. (1987) found that low starch reserves increase the vulnerability of white oaks to twolined chestnut borer. We found that trees of low vigour, as reflected by crown condition, intercepted greater numbers of twolined chestnut borer than trees with relatively vigorous crowns (Table 5). However, we found no differences between trees with poor crown condition and trees with fair crown condition. Trees with declining crown condition, irrespective of extent of decline, were equally vulnerable to twolined chestnut borer.

Previous research on the host preference of twolined chestnut borer suggests that, although nearly restricted to oaks and chestnut, twolined chestnut borer attacked beech (probably *Fagus grandifolia*) in Massachusetts (Faull, 1936). Chapman (1915) suggested that black oak (a member of the red oak group) was a favoured host, and Decker (1933) concluded that red oak was preferred. Kegg (1973) and Dunbar & Stephens (1975) found that white oaks were highly vulnerable to twolined chestnut borer, and Côté & Allen (1980) reported that chestnut oak (a member of the white oak group) had the greatest number of twolined chestnut borers compared with red, black and white oaks. We found that the red oak group attracted significantly more twolined chestnut borer than the white oak group; this was particularly true for trees with poor or fair crowns. All oaks seem to be hosts of the twolined chestnut borer, and factors such as species dominance in the overstory, site conditions, as well as physiological condition, may all play a role in determining host suitability.

As twolined chestnut borers are attracted to stressed trees, removal of overstory trees of low vigour and low starch reserves (Dunn *et al*., 1990), may maintain low populations of twolined chestnut borer. Thinning an overstocked stand to increase vigour of the residual trees represents an approach to minimize susceptibility. Stress and injury associated with thinning, however, may cause twolined chestnut borer populations to increase, at least temporarily. Until crowns recover and exploit resources released by thinning, there may be increases in twolined chestnut borer and mortality even in the absence of an additional stressor, such as gypsy moth defoliation. Chapman (1915) noted that light influences oviposition of twolined chestnut borer; thus, canopy opening and increased light may influence twolined chestnut borer abundance. Timing of silvicultural treatments is important, however, because thinning a stand during the summer aids in cambial dessication of the cut material, and may destroy existing larvae (Haack & Acciavatti, 1992). The stands on the WVUF were logged in the autumn and winter, and therefore had no adverse affect on the twolined chestnut borer larvae that were present at the time of logging. Although little can be done to mitigate the effects of defoliation, silvicultural practices to increase overall stand vigour, if timed appropriately, may limit the potential increases in twolined chestnut borer populations, particularly the increases attributed to logging activity. Furthermore, this study demonstrated that twolined chestnut borer activity may be relatively limited temporally and spatially, and that abundance in a given area does not necessarily lead to large increases and subsequent overstory mortality in the surrounding forest.

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References

Arnett, R.H. (1993) American insects. *A Handbook of the Insects of America North of Mexico.* The Sandhill Crane Press, Gainesville.

Chapman, R.N. (1915) Observations on the life history of *Agrilus bilineatus*. *Journal of Agricultural Research*, **3**, 283–293.

Chittenden, F.H. (1909) *The Twolined chestnut borer*. USDA Bureau of Entomology Circular no. 24.

Côté, W.A. (1976) *The biology of the two-lined chestnut borer and its impact on defoliated oaks*. PhD Thesis, State University of New York, Syracuse, New York.

Côté, W.A. & Allen, D.C. (1980) Biology of two-lined chestnut borer, *Agrilus bilineatus,* in Pennsylvania and New York. *Annals of the Entomological Society of America*, **73**, 409–413.

Decker, G.C. (1933) The two-lined chestnut borer and its control. *Iowa State Horticultural Society Report*, **68**, 151–156.

Dunbar, D.M. & and. Stephens, G.R. (1976) The bionomics of the Twolined Chestnut Borer. *Perspectives in Forest Entomology* (ed. by J. E. Anderson and H. K. Kaya), pp. 73–83. Connecticut Agricultural Experiment Station, New Haven, CT.

Dunbar, D.M. & Stephens, G.R. (1975) Association of twolined chestnut borer and shoestring fungus with mortality of defoliated oak in Connecticut. *Forest Science*, **21**, 169–174.

Dunn, J.P., Kimmerer, T.W. & Nordin, G.L. (1986) Attraction of the twolined chestnut borer *Agrilus bilineatus*, (Weber) (Coleoptera: Buprestidae), and associated borers to volatiles of stressed white oak. *Canadian Entomologist*, **118**, 503–509.

Dunn, J.P., Kimmerer, T.W. & Potter, D.A. (1987) Winter starch reserves of white oak as a predictor of attack by the twolined chestnut borer, *Agrilus bilineatus* (Weber) (Coleoptera: Buprestidae). *Oecologia*, **74**, 352–355.

Dunn, J.P., Potter, D.A. & Kimmerer, T.W. (1990) Carbohydrate reserves, radial growth, and mechanism of resistance of oak trees to phloem-boring insects. *Oecologia*, **83**, 458–468.

Faull, J.H. (1936) Pathological studies on beech at the Arnold Arboretum. 2. Cankers caused by the twolined chestnut borer, *Agrilus bilineatus*. *Proceedings of the National Shade Tree Conference*, pp. 25–27.

Gottschalk, K.W. (1993) *Silvicultural Guidelines for Forest Stands Threatened by the Gypsy Moth.* USDA Forest Service General Technical Report NE-171.

Haack, R.A. & Acciavatti, R.E. (1992) *Twolined chestnut borer*. USDA Forest Service Forest Insect and Disease Leaflet 168.

Haack, R.A. & Benjamin, D.M. (1982) The biology and ecology of the twolined chestnut borer, *Agrilus bilineatus* (Coleoptera: Buprestidae), on oaks, *Quercus* spp., in Wisconsin. *Canadian Entomologist*, **114**, 385–396.

Haack, R.A., Benjamin, D.M. & Haack, K.D. (1983) Buprestidae, cerambycidae, and scolytidae associated with successive stages of *Agrilus bilineatus* (Coleoptera: Buprestidae) infestation of oaks in Wisconsin. *Great Lakes Entomologist*, **16**, 47–55.

Kegg, J.D. (1973) Oak mortality caused by repeated gypsy moth defoliation of oak in New Jersey. *Journal of Economic Entomology*, **66**, 639–641.

Liebhold, A.M., Muzika, R.M. & Gottschalk, K.W. (1998) Does thinning affect gypsy moth dynamics? *Forest Science*, **44**, 239–245.

Staley, J.M. (1965) Decline and mortality of red and scarlet oaks. *Forest Science*, **11**, 2–17.

Wargo, P.M. (1977) *Armillariella mellea* and *Agrilus bilineatus* and mortality of defoliated oak trees. *Forest Science*, **23**, 485–492.

Wargo, P.M., Houston, D.R. & LaMadeleine, L.A. (1983) *Oak Decline.* USDA Forest Service Forest Insect and Disease Leaflet 165.

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